A cytotaxonomic study of *Lantana camara* (Verbenaceae) from South Africa

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Numerical taxonomical methods were applied to the cytological data obtained from 97 *Lantana camara* L. plants. This resulted in the delimitation of 11 cytogroups at three polyploid levels. No correlation was found to exist between the cytological data and plant morphology. The cytological data demonstrated that *L. camara* is in an active evolutionary phase and, because most plants are intermediates in a transitional stage of speciation, no attempt to recognize infraspecific entities will succeed.

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Numeriese taksonomiese metodes is toegepas op die sitologiese data wat van 97 *Lantana camara* L. plante verkry is. Hierdie resultate het die afbakening van 11 sitogroepe op drie poliploïede vlakke tot gevolg gehad. Geen verband kon tussen die sitologiese data en plantmorfologie gevind word nie. Die sitologiese data toon aan dat *L. camara* in 'n aktiewe evolusionêre fase is. Omdat die meeste plante tussenvorme in 'n oorgangsfase van 'n spesiasie-proses is, sal geen poging om groepe onder spesievlak te identifiseer slaag nie.

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Keywords: Chromosome, cytotaxonomy, evolution, *Lantana camara*, numerical taxonomy, polyploidy

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Introduction

Lantana camara L. is a New World species which now has an almost worldwide distribution. The generic epicentre is regarded as being Mexico and Central America (Smith 1970), from where *L. camara* has been introduced to the rest of the world via Europe (Stirton 1977).

L. camara sensu lato presents a complex taxonomical problem owing to the considerable morphological variation present within this species. This variation, in particular the many colour forms, has led to the description of more than 650 cultivars (Howard 1969). These taxa were not distinguished by clear morphological differences and several nomenclatural ambiguities were also included (Stirton 1977).

Initially this variability in *L. camara* was attributed to apomixis and polyploidy (Stirton 1977). The suggestion that apomixis occurs in this species (Raghavan & Arora 1960; Khoshoo & Mahal 1967) has not been confirmed by cytological studies, which have proved that all *L. camara* plants reproduce sexually (Junell 1934; Patermann 1935; Tatachar 1940; Crété 1942; Padmandabhan 1959; Khaleel & Nalini 1972; Spies & Stirton 1982a; Spies 1984b & e).

The potential for hybridization was first inferred by Moldenke (1971) and later demonstrated by Spies (1984c). Further proof of hybridization within this species has been reported from South Africa where a total collapse of isolating mechanisms between different forms of *L. camara* has resulted in the formation of a hybrid swarm in the Eastern Transvaal lowveld near White River (Spies 1984e). Further indications are that extensive hybridization within this complex occurs throughout the distribution range of *L. camara* in South Africa (Spies 1984e).

Hybridization results in the continuous variation of characters between the parental extremes, and the hybrids may even exceed the parents in some instances. This fact is responsible for the exceedingly difficult task of classifying a hybrid complex according to normal morphological taxonomic procedures. In an attempt to solve this problem a cytological study was carried out on *L. camara* (Spies & Stirton 1982b & c; Spies 1984e). The aim of the present study is to use these cytological data as a basis for a preliminary taxonomical treatment of the *L. camara* complex as represented in South Africa.

Materials and Methods

L. camara plants were collected mainly from a hybrid swarm

near White River in the Eastern Transvaal lowveld and transplanted in the National Botanical Garden, Pretoria. Herbarium voucher specimens of the following cytologically examined plants are stored in the Pretoria National Herbarium (PRE):

TRANSVAAL. — 2330 (Tzaneen): 10 km from Tzaneen to Duiwelskloof (–CA), *Stirton 5710*; 9 km from Tzaneen to Phalaborwa (–CC), *Stirton 5759, 5760, 5784*. 2428 (Nylstroom): 10 km from Nylstroom to Naboomspruit (–DA), *Stirton 5704*. 2528 (Pretoria): Pretoria North (–CA), *Stirton 7229, 7230, 7231, 7253*. 2530 (Lydenburg): 6 km from Nelspruit to Barberton (–BD), *Stirton 6822*. 2531 (Komatipoort): Glory Hill Guest Farm (–AA), *Stirton 7054, 7055, 7058, 7060, 7061, 7062, 7087, 7430, 7431, 7432*; 20 km from Numbi to White River (–AA), *Stirton 7351, 7361, 7369, 7371, 7374*; 38 km from White River to Hazyview (–AA), *Stirton 7377, 7381, 7382, 7383, 7384, 7387, 7389, 7390, 7393, 7394, 7395, 7396, 7397, 7398, 7399*; 6 km from White River to Hazyview (–AC), *Stirton 6875, 6877, 6878, 6879, 6881, 6882, 6883, 7064, 7065, 7066, 7067, 7068, 7069, 7071, 7104, 7270, 7289, 7292, 7293, 7294, 7295, 7296*; near Klipkopjes (–AC), *Stirton 7302, 7303, 7304, 7305, 7306, 7307, 7308, 7311, 7312, 7314, 7315, 7316, 7328, 7332, 7338, 7339, 7343, 7345, 7348*; 8 km from Plaston to Karino (–CA), *Stirton 7408*; 25 km from Nelspruit to Komatipoort (–CB), *Stirton 6782, 6784, 6791*; 30 km from Nelspruit to Barberton (–CC), *Stirton 6837*.

NATAL. — 2831 (Nkandla): near Eshowe (–CD), *Stirton 5287, 5288*; 5 km from Nkwaleni to Empangeni (–DA), *Stirton 5280*. 2930 (Pietermaritzburg): 19 km from Thornville to Eston (–CD), *Stirton 5438*; near Nagledam (–DA), *Stirton 5400*. 2931 (Stanger): Tugela Mouth (–AB), *Stirton 5352*. 3030 (Port Shepstone): Port Edward (–CD), *Stirton 8727*. 3130 (Port Edward): 15 km from Port Edward to Bizana (–AA), *Stirton 5605*.

CAPE. — 3418 (Simonstown): near Simonstown (–BB), *Stirton 5832*; near Hermanus (–BD), *Stirton 5831*. 3422 (Mossel Bay): near Mossel Bay (–AA), *Stirton 6324*.

Meiotic material was only collected from the transplanted plants so as to minimize possible environmental effects on the chromosomal behaviour. The cytological methods used and data obtained have been partially published (Spies & Stirton 1982b & c).

The cytological data mentioned above were used as numerical values for the NT-SYS program (Numerical taxonomy system of multi-variate statistical programs) of Rohlf *et al.* (1977). Dendrograms were determined by using the average taxonomic distance (ATD) which is computed as the square root of the average squared difference between two variables (Sokal 1961; Sokal & Sneath 1963). All calculations were done by using the unweighted pair-group method with arithmetic averages.

Only a limited number of characters could be evaluated owing to the physical restriction on the size of the matrix that could be analysed. For this study the average percentage of chromosomes bound as I, II, III, etc., chiasma frequency (average number of chiasmata per bivalent) and the number of cells exhibiting each type of chromosome association were used to determine basic attributes. Between 20 and 25 cells per plant were analysed during this study of microsporogenesis. Every polyploid level was treated separately because the additional chromosomes at each higher polyploid level make comparison between different levels impractical. All computer work was done on a CDC computer at the CSIR (Pretoria).

Results and Discussion

The cytological data showed that chromosome numbers of 2n = 22, 33, 44, 55 and 66 are found in the *Lantana camara* complex. In addition, plants showed great variation with respect to chromosome associations, chiasma frequencies and number of cells exhibiting each type of chromosome association at each polyploid level. The data used for the numerical analysis are shown in Tables 1, 2, 4, 5, 7 & 8.

The dendrograms obtained for the 2n = 22, 33 and 44 plants are shown respectively in Figures 1, 5 & 9. An increase in the ATD values indicates a decrease in similarity and, therefore, two plants with a high ATD are not closely related whereas plants with a low ATD show closer relationships. The correlations for the different polyploid levels

Table 1 Chromosome associations and chiasma frequencies in 2n = 22 chromosome plants

Stirton no.	2n=	No. cells analysed	% of Chromosomes bound as I	II	III	IV	Number of chiasmata/ bivalent
2264	22	20	9,55	79,55	10,41	–	1,01
5760	22	25	5,27	90,18	3,82	0,73	1,08
5784	22	20	2,73	97,27	–	–	1,21
6882	22	25	0,36	99,64	–	–	1,17
7062	22	25	6,91	90,91	2,18	–	1,01
7066	22	25	–	100	–	–	1,09
7068	22	25	19,27	74,18	6,55	–	0,94
7069	22	25	4,91	93,45	1,64	–	1,13
7071	22	25	4,18	94,18	1,64	–	1,04
7231	22	20	6,36	87,27	5,45	0,91	1,02
7289	22	25	6,18	91,64	2,18	–	1,03
7292	22	25	12,55	84,73	2,73	–	1,11
7293	22	20	4,55	94,09	1,36	–	1,04
7294	22	25	2,18	95,64	2,18	–	1,1
7295	22	25	9,45	87,27	3,27	–	1,18
7296	22	25	1,45	93,09	5,45	–	1,09
7302	22	25	33,09	62,55	4,36	–	0,68
7303	22	25	6,55	92,36	1,09	–	0,99
7304	22	25	4,55	93,82	1,64	–	1,05
7305	22	25	2,91	97,09	–	–	1,08
7306	22	25	9,64	85,45	4,91	–	1,07
7307	22	25	–	100	–	–	1,22
7308	22	25	6,55	93,45	–	–	1,07
7311	22	25	9,82	89,09	1,09	–	0,93
7314	22	20	21,14	75,45	3,41	–	0,84
7315	22	20	18,41	75,45	6,14	–	0,94
7316	22	25	3,45	94,91	1,64	–	1,19
7328	22	25	13,09	84,73	2,18	–	0,96
7332	22	25	4,18	94,18	1,64	–	1,07
7338	22	25	5,82	94,18	–	–	0,96
7339	22	20	11,82	85,45	2,73	–	1,01
7343	22	25	4,36	95,64	–	–	1,03
7345	22	25	10,73	84,36	4,91	–	1,03
7361	22	20	10,68	88,64	0,68	–	0,95
7369	22	20	11,59	70	18,41	–	0,99
7371	22	25	4,18	95,27	0,55	–	1,01
7374	22	20	0,91	99,09	–	–	1,15
7389	22	20	5,45	93,18	1,36	–	1,05
7390	22	25	3,27	94,55	2,18	–	1,03
7395	22	25	6,18	92,73	1,09	–	0,96
7396	22	25	1,09	98,91	–	–	1,13
7397	22	25	1,82	97,09	1,09	–	1,11
7399	22	25	2,36	97,09	0,55	–	0,98
$\bar{x}$	22	23,72	7,2	90,18	2,58	0,04	1,04

were: 2n = 22 – 0,981; 2n = 33 – 0,894 and 2n = 44 – 0,821.

By using the three main characters responsible for separating the different plants into their clusters (Principal component analysis), a three dimensional representation of the actual 'distance' between the different plants can be obtained. In the 2n = 22 group the accumulated percentage of influence of the three main factors was 55,26%. This procedure gave an accumulated percentage of 45,19% for the 2n = 33 group. In the 2n = 44 group this percentage reached 57,03%. The plotting of these factors against one another can be seen in Figures 2, 3, 4, 6, 7, 8, 10, 11 & 12. These data were used to construct a minimum spanning tree for each polyploid level (Tables 3, 6 & 9) to determine the closest relationship between individual plants.

The combination of the dendrogram, principal component analysis and minimum spanning tree results enabled the identification of several cytogenetic groups or cytogroups. As comparison between the different polyploid levels is extremely difficult owing to cytogenetical considerations, the different ploidy levels will be discussed separately.

1. The 2n = 22 chromosome group

This group consists of 43 plants of a heterogeneous morphological and cytological nature. An average of 1,58 univalents (s = 1,42) per cell was encountered. This number varied from 0 in *Stirton 7066* and *7307* to 7,28 in *Stirton 7302*. The number of bivalents ranged from 62,55% in *Stirton 7302* to 100% in *Stirton 7066* and *7307*, with an average of 90,18% (s = 0,93) bivalents per cell (Table 1). Trivalents were present in 76,7% of the examined plants. Quadrivalents were present in two plants, *Stirton 5760* and *7231*, with 0,04% and 0,05% per cell respectively.

The same heterogeneous nature of the chromosome associations found in the 2n = 22 chromosome group was also evident in the chiasma frequency (Table 1) and cell distribution frequency of each type of chromosome association (Table 2). Correlations between different plants, using cell frequency data, indicated the existence of cytological groupings within this diploid group (Spies & Stirton 1982c). This led to the application of a numerical taxonomic analysis on all the data to establish the relationships within the different ploidy levels. By using 0,88 as the phenon line (Figure 1) and by including data from both principal component analysis (Figures 2–4) and the minimum spanning tree (Table 3), the following cytogroups can be distinguished:

1.1 Group α

This group consists of *Stirton 5784, 6882, 7062, 7066, 7069, 7071, 7289, 7293, 7294, 7303, 7305, 7307, 7308, 7316, 7332, 7338, 7343, 7371, 7374, 7389, 7390, 7395, 7396, 7397* and *7399*. With the exception of *Stirton 5784*, which was collected near Tzaneen, all plants were collected from the White River hybrid complex. This complex occupies the grid squares 2530BD, 2531AA, 2531AC, 2531CA, 2531CB and 2531CC.

Group *α* has an average chromosome association of $0{,}8_{I}\ 10{,}5_{II}\ 0{,}07_{III}$ and a chiasma frequency of 1,07. This group is characterized by its high frequency of bivalents (88,1% of the cells studied contained at least 10 bivalents). The lowest percentage of bivalents in any individual plant of this group was 90,91% (*Stirton 7062*). Plants belonging to the *α* group are distinguished by the fact that they have less than 20% cells containing a trivalent and more than 70% cells with 10 or 11 bivalents.

1.2 Group β

This group consists of *Stirton 7292, 7295, 7306, 7311, 7328,* 7339 and *7361* and all these plants were collected from the White River complex. The plants in group *β* are characterized by their high frequency of univalents. The average chromosome association of this group is $2{,}4_{I}\ 9{,}5_{II}\ 0{,}18_{III}$ with an average chiasma frequency of 1,03. Ten or 11 bivalents were

Table 2 Chromosome associations per cell in 2n = 22 chromosome plants

Chromosome association	2264	5760	5784	6882	7062	7066	7068	7069	7071	7231	7289	7292	7293	7294	7295	7296	7302	7303	7304	7305	7306	7307	7308	7311	7314	7315	7316	7328	7332	7338	7339	7343	7345	7361	7369	7371	7374	7389	7390	7395	7396	7397	7399	Total
11_{II}	4	8	14	24	8	25	2	11	14	7	9	6	12	18	8	16	–	11	16	17	7	25	11	12	–	4	15	4	15	12	6	14	8	7	3	16	18	10	14	12	22	19	18	502
$10_{II}2_{I}$	5	8	6	1	10	–	3	10	7	6	11	6	3	3	5	1	–	7	4	8	7	–	10	5	2	–	8	8	5	10	6	10	8	5	1	6	2	5	7	7	3	4	6	229
$9_{II}4_{I}$	–	2	–	–	3	–	4	1	–	1	–	6	3	–	5	–	2	5	3	–	2	–	4	2	7	4	–	6	1	3	2	1	1	3	1	1	–	3	–	4	–	–	–	80
$9_{II}1_{I}1_{III}$	4	5	–	–	3	–	3	3	3	4	3	2	2	3	3	6	–	2	1	–	3	–	–	–	1	–	–	1	3	–	–	–	1	1	1	1	–	2	4	1	–	2	1	69
$9_{II}1_{IV}$	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1
$8_{II}6_{I}$	–	–	–	–	–	–	4	–	1	1	1	2	–	–	2	–	5	–	–	–	–	–	–	4	3	3	–	3	1	–	1	–	–	4	–	1	–	–	–	–	–	–	–	36
$8_{II}3_{I}1_{III}$	2	–	–	–	1	–	2	–	–	–	1	1	–	1	1	–	–	–	–	–	2	–	–	–	2	2	1	1	–	–	2	–	2	–	6	–	–	–	–	1	–	–	–	28
$8_{II}2_{III}$	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	2	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	4
$7_{II}8_{I}$	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	8	–	–	–	–	–	–	–	2	–	–	–	–	–	1	–	1	–	–	–	–	–	–	–	–	–	–	12
$7_{II}5_{I}1_{III}$	3	–	–	–	–	–	3	–	–	–	–	1	–	–	–	–	–	–	–	–	3	–	–	1	2	4	–	2	–	–	1	–	1	–	2	–	–	–	–	–	–	–	–	23
$7_{II}2_{I}2_{III}$	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	1
$6_{II}10_{I}$	–	–	–	–	–	–	2	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	4
$6_{II}7_{I}1_{III}$	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	7	–	–	–	1	–	–	1	–	3	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	13
$6_{II}4_{I}2_{III}$	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	3
$6_{II}1_{I}3_{III}$	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	1	–	–	–	–	–	–	–	2
$5_{II}12_{I}$	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1
$5_{II}9_{I}1_{III}$	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	2	–	–	–	–	–	–	–	–	–	–	3
$5_{II}6_{I}2_{III}$	1	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	2
$5_{II}3_{I}3_{III}$	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	2	–	–	–	–	–	–	–	–	2
$4_{II}11_{I}1_{III}$	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1
$3_{II}10_{I}2_{III}$	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1
$3_{II}1_{I}5_{III}$	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1
$2_{II}3_{I}5_{III}$	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	1
$2_{II}2_{I}4_{III}1_{IV}$	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1

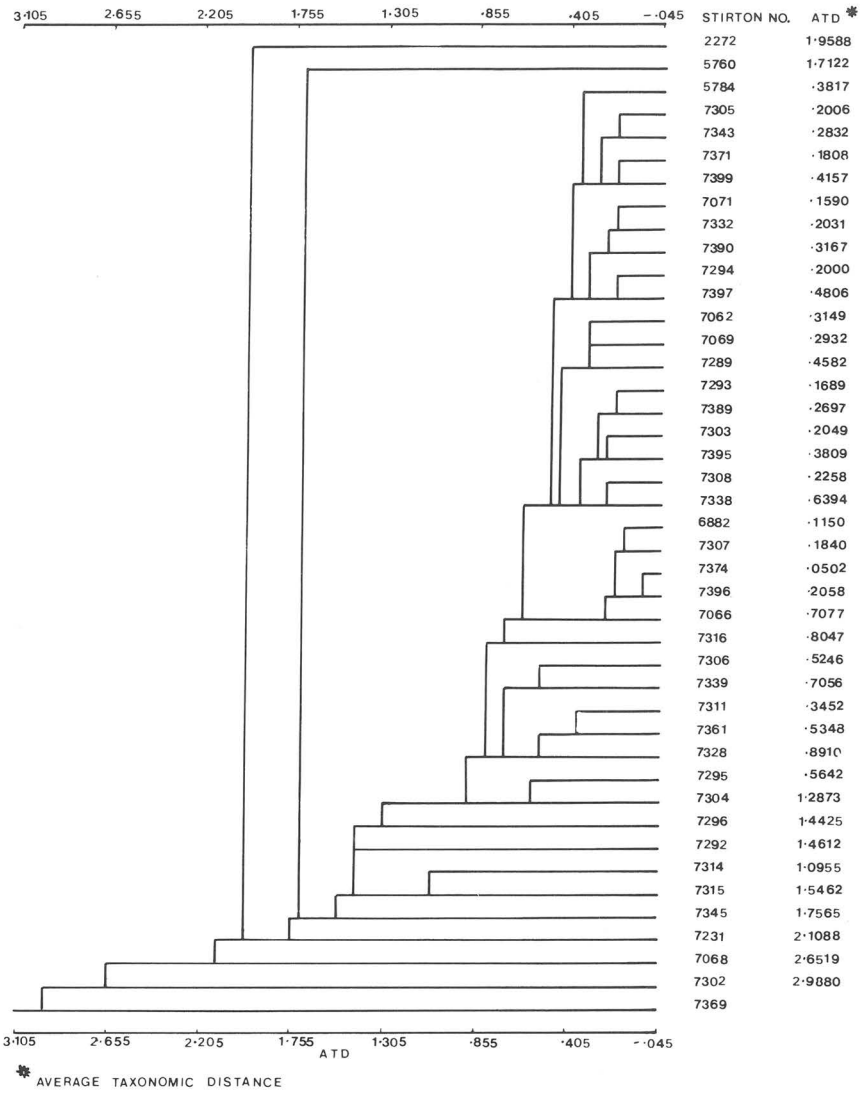

Figure 1 Cytological based dendrogram of 2n = 22 chromosome *Lantana camara* plants.

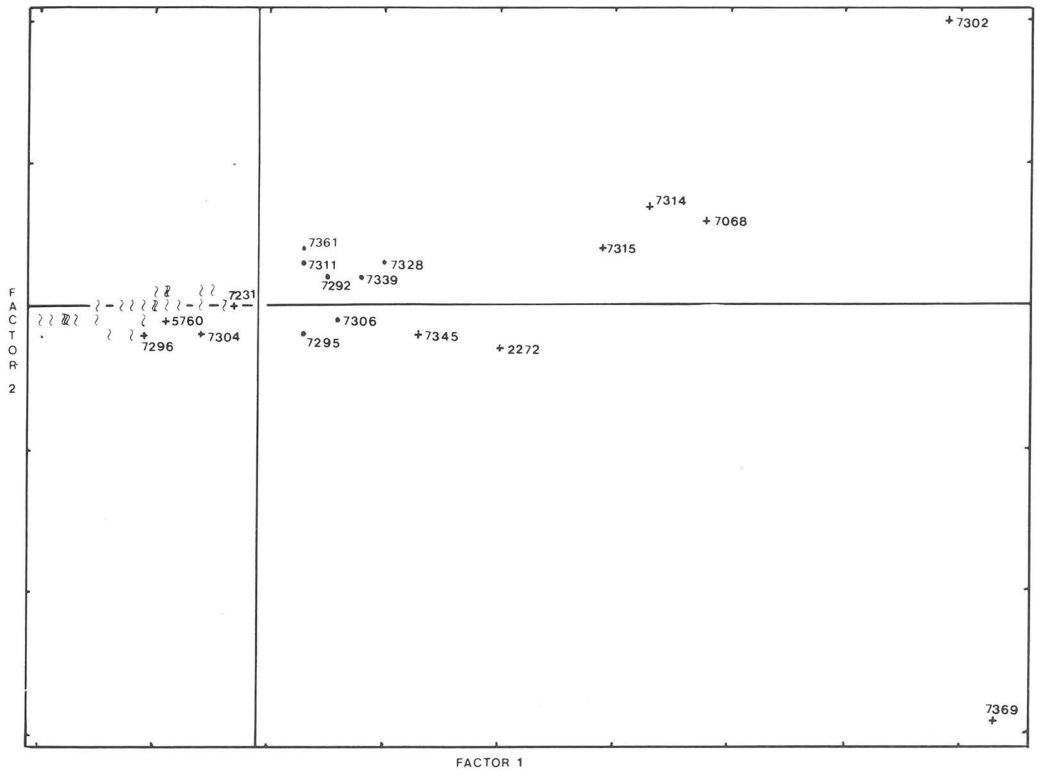

Figure 2 Cytological based principal component analysis of 2n = 22 chromosome *Lantana camara* plants.

encountered in only 55,7% of the cells examined. The percentage of bivalents in this group ranged from 84,7% in *Stirton 7292* and *7328*, to 89,09% in *Stirton 7311*. The percentage of cells containing at least one trivalent reached 23,65%.

1.3 Group γ

All plants with 22 somatic chromosomes but not included in either the α or β groups, are included in the γ group. This group comprises *Stirton 5760, 7068, 7231, 7296, 7302, 7304, 7314, 7315, 7345* and *7369*. With the exception of *Stirton 5760*, collected near Tzaneen, and *Stirton 7231*, collected near Pretoria, all these plants were collected from the White River hybrid swarm. As no close relationship exists between any two of these plants, this is only a conglomerate of plants with no common character binding them together.

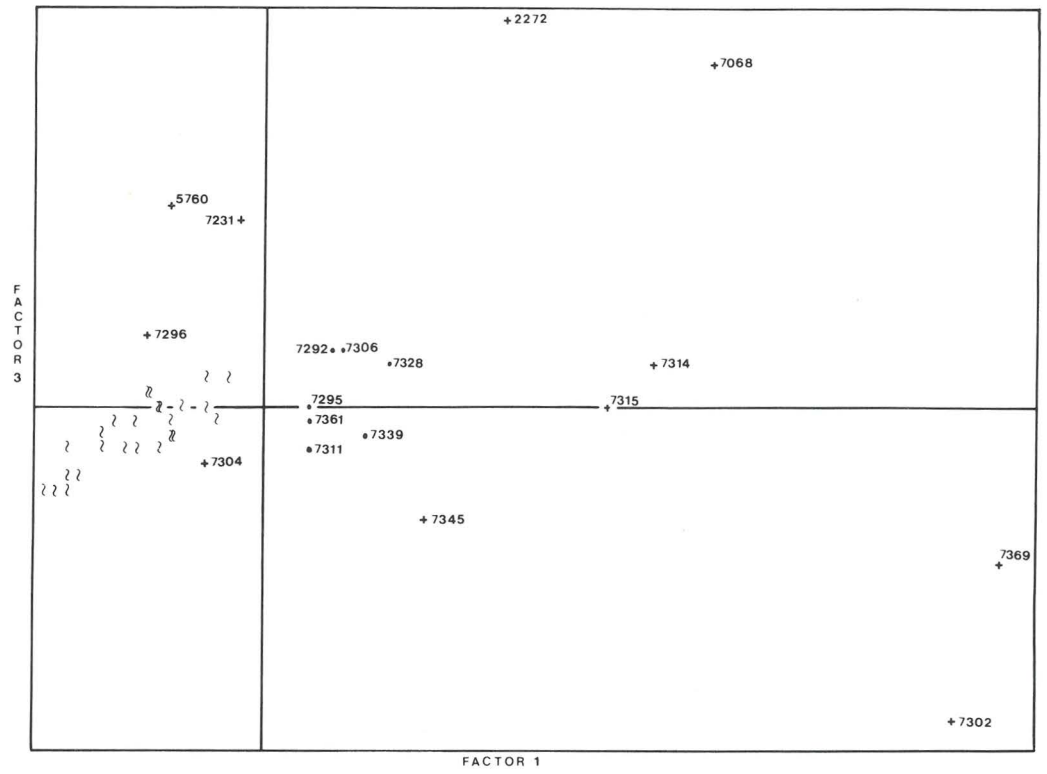

Figure 3 Cytological based principal component analysis of 2n = 22 chromosome *Lantana camara* plants.

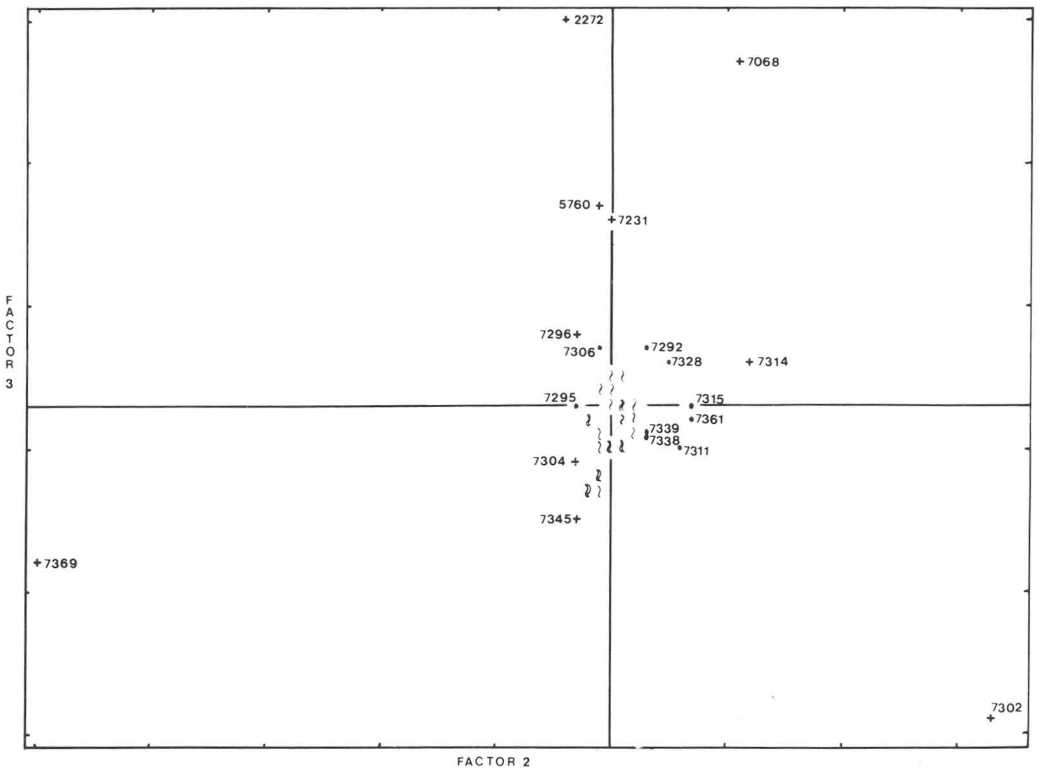

Figure 4 Cytological based principal component analysis of 2n = 22 chromosome *Lantana camara* plants.

Table 3 The minimum spanning tree for 2n = 22 chromosome plants

Stirton no.	Stirton no.	ATD
2272	7306	1,634
7306	7339	0,525
7339	7395	0,533
7395	7303	0,205
7303	7389	0,18
7389	7293	0,169
7395	7338	0,272
7338	7308	0,226
7338	7343	0,229
7343	7305	0,201
7305	5784	0,245
7305	7399	0,251
7399	7371	0,181
7371	7332	0,263
7332	7071	0,159
7071	7390	0,169
7332	7397	0,257
7397	7294	0,2
7397	7396	0,257
7396	7374	0,05
7374	6882	0,107
6882	7307	0,115
6882	7066	0,164
7071	7069	0,3
7069	7289	0,293
7289	7062	0,294
7371	7311	0,531
7311	7361	0,345
7361	7328	0,506
5784	7316	0,543
7293	7304	0,685
7304	7295	0,564
7328	7314	0,938
7328	7315	0,972
7316	7296	0,983
7328	7292	1,277
7339	7345	1,384
7390	5760	1,561
7390	7231	1,595
7314	7068	1,62
7314	7302	2,127
7306	7369	2,739

Table 4 Chromosome associations and chiasma frequencies in 2n = 33 chromosome plants

Stirton no.	2n=	No. cells analysed	% of Chromosomes bound as I	II	III	IV	Number of chiasmata/ bivalent
5759	33	25	8,85	39,76	50,91	0,48	1,11
6837	33	20	8,48	51,52	40	—	1,09
6875	33	25	11,88	43,88	43,27	0,97	1,13
6878	33	20	10,45	58,18	31,36	—	1,2
6883	33	20	7,58	60,61	31,82	—	1,16
7067	33	20	7,73	72,73	19,55	—	1,14
7348	33	20	8,03	54,55	36,82	0,61	1,15
7381	33	20	3,79	83,94	12,27	—	1,17
7382	33	20	12,88	64,85	22,27	—	1,06
7383	33	20	8,94	73,64	16,82	0,61	1,07
7384	33	20	16,67	60	22,73	0,61	1,05
7387	33	20	8,18	65,45	26,36	—	1,11
7393	33	25	15,64	63,27	21,09	—	1,03
7394	33	25	14,3	50,42	35,27	—	1,09
7398	33	20	10,3	61,52	28,18	—	1,07
$\bar{x}$	33	21,33	10,25	60,29	29,25	0,22	1,11

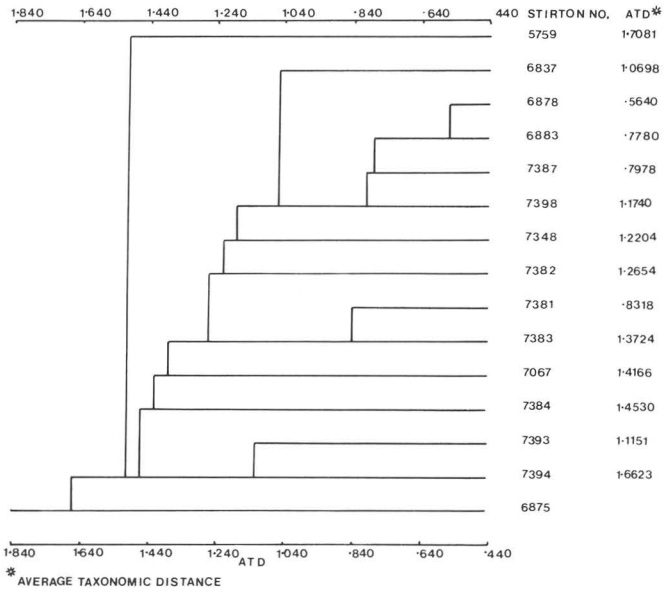

Figure 5 Cytological based dendrogram of 2n = 33 chromosome *Lantana camara* plants.

2. The 2n = 33 chromosome group

The 15 plants included in this group exhibit heterogeneous cytogenetic behaviour. The average percentage of univalents (10,25% − s = 3,46) varied from 3,79% in *Stirton 7381* to 16,67% in *Stirton 7384* (Table 4). The number of bivalents varied from 39,76 in *Stirton 5759* to 83,94% in *Stirton 7381*, with an average of 60,29% (s = 11,5). Trivalents ranged from 12,27% in *Stirton 7381* to 50,91% in *Stirton 5759* with an average of 29,25% (s = 10,66). An occasional quadrivalent was observed in *Stirton 5759, 6875, 7348, 7383* and *7384* but the number never exceeded 1%.

A combination of the dendrogram (Figure 5), principal component analysis (Figures 6–8) and minimum spanning tree (Table 6) resulted in the identification of four cytogroups in the studied material.

2.1 Group δ

Stirton 6878, 6883, 7387 and *7398* are the components of this group which was collected entirely from the White River complex. This group has an average chromosome association of $3{,}01_{I}\ 10{,}14_{II}\ 3{,}24_{III}$ with an average chiasma frequency of 1,14 (Table 4). The chromosome association per cell varied from $1_{I}\ 13_{II}\ 2_{III}$ to $2_{I}\ 8_{II}\ 5_{III}$ with $4_{I}\ 10_{II}\ 3_{III}$ and $3_{I}\ 9_{II}\ 4_{III}$ being the most frequent (Table 5).

2.2 Group ϵ

Both plants in this group, *Stirton 7381* and *7383*, were collected from the White River complex. An average chromosome association of $2{,}1_{I}\ 13_{II}\ 1{,}6_{III}\ 0{,}03_{IV}$ and a chiasma frequency of 1,12 were observed in this group (Table 4). The chromosome associations per cell varied from

$15_{II}\,1_{III}$ to $8_I\,5_{II}\,5_{III}$ with $15_{II}\,1_{III}$ and $1_I\,13_{II}\,2_{III}$ in the majority of the cells (Table 5).

2.3 Group ζ

This group consists of *Stirton 7393* and *7394* which were both collected from the White River complex. Group ζ has an average chromosome association of $4{,}9_I 9{,}38_{II} 3{,}1_{III}$ and a chiasma frequency of 1,06 (Table 4). The cell chromosome association varied extensively from cell to cell to such a degree that 41,03% of the different associations encountered in 2n = 33 plants, were present in this group. These associations varied from $2_I\,14_{II}\,1_{III}$ to $2_I\,5_{II}\,7_{III}$ (Table 5).

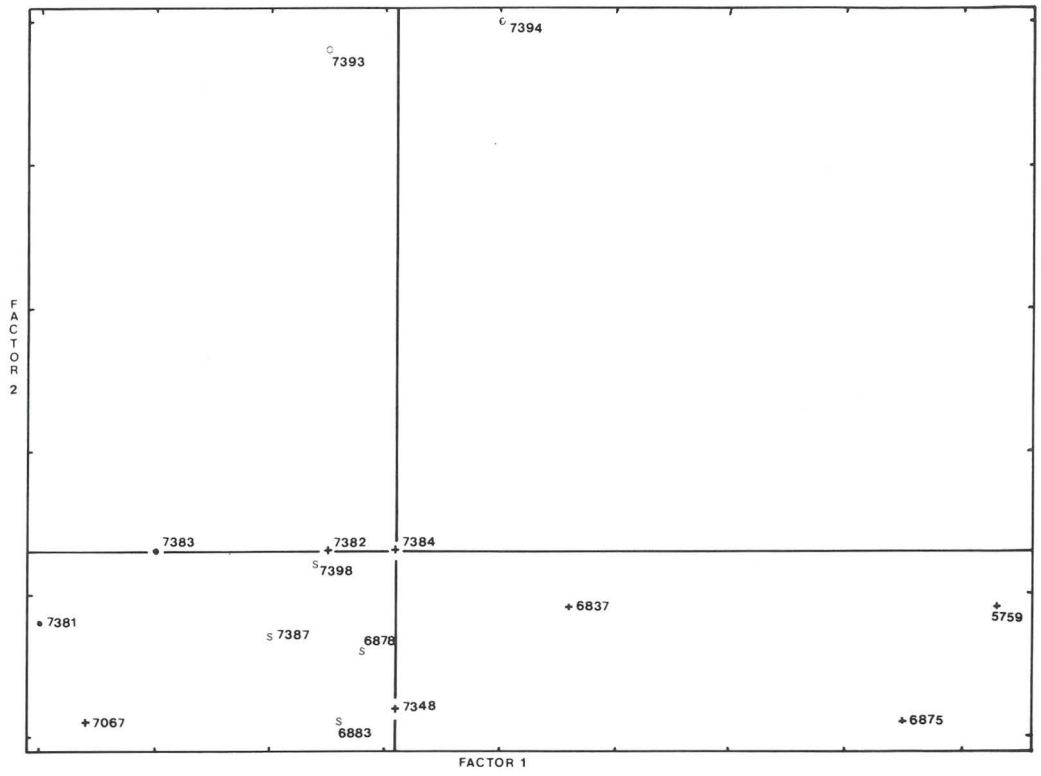

Figure 6 Cytological based principal component analysis of 2n = 33 chromosome *Lantana camara* plants.

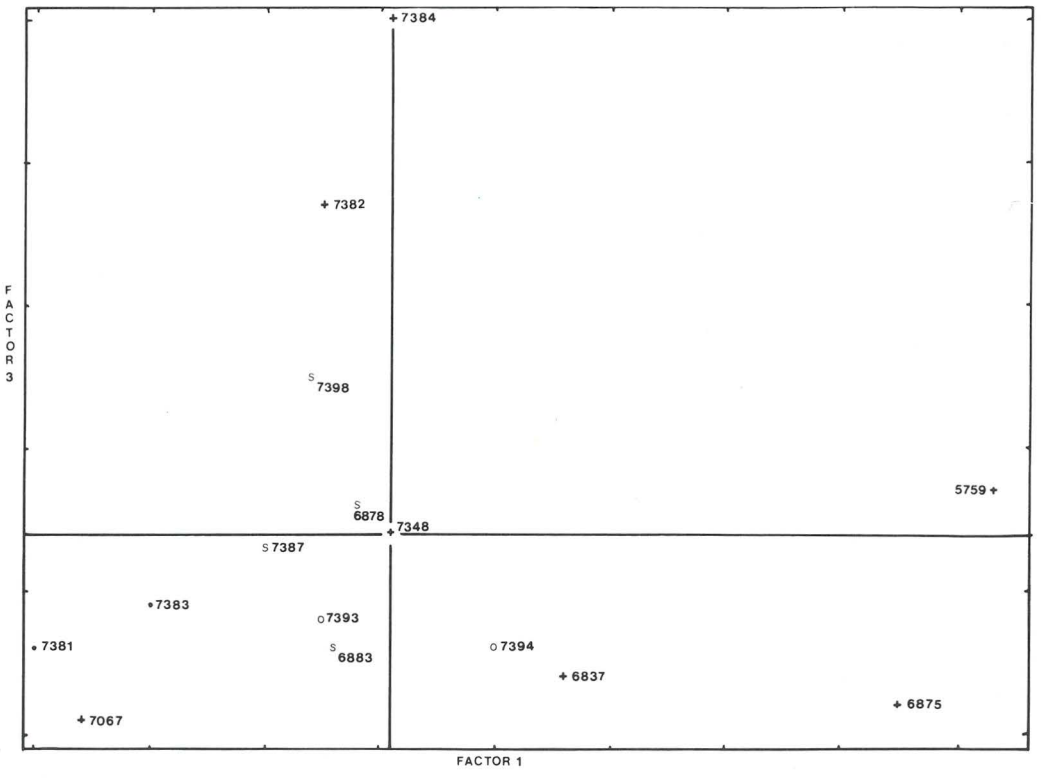

Figure 7 Cytological based principal component analysis of 2n = 33 chromosome *Lantana camara* plants.

2.4 Group η

Stirton 5759, 6837, 6875, 7067, 7348, 7382 and *7384* are grouped together in this reject dump of the 2n = 33 group. The only mutual character of the η group is that none of these plants are related to one another nor to any of the other groups. *Stirton 5759* was collected near Tzaneen whereas all the other plants were collected from the White River complex.

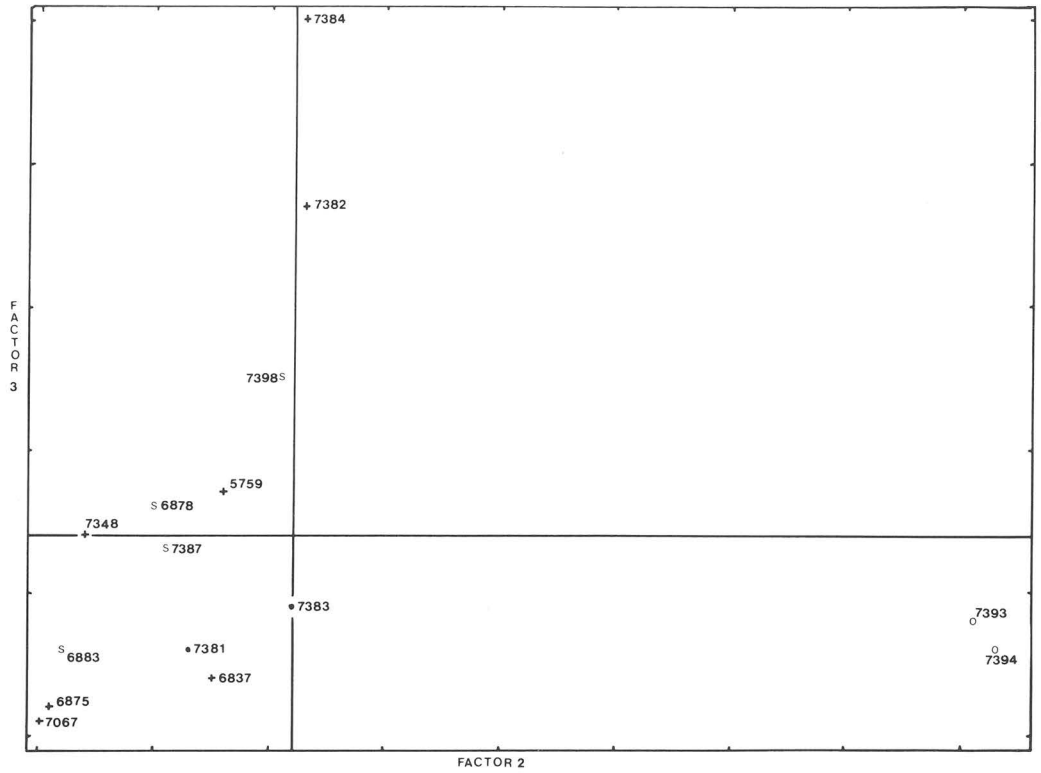

Figure 8 Cytological based principal component analysis of 2n = 33 chromosome *Lantana camara* plants.

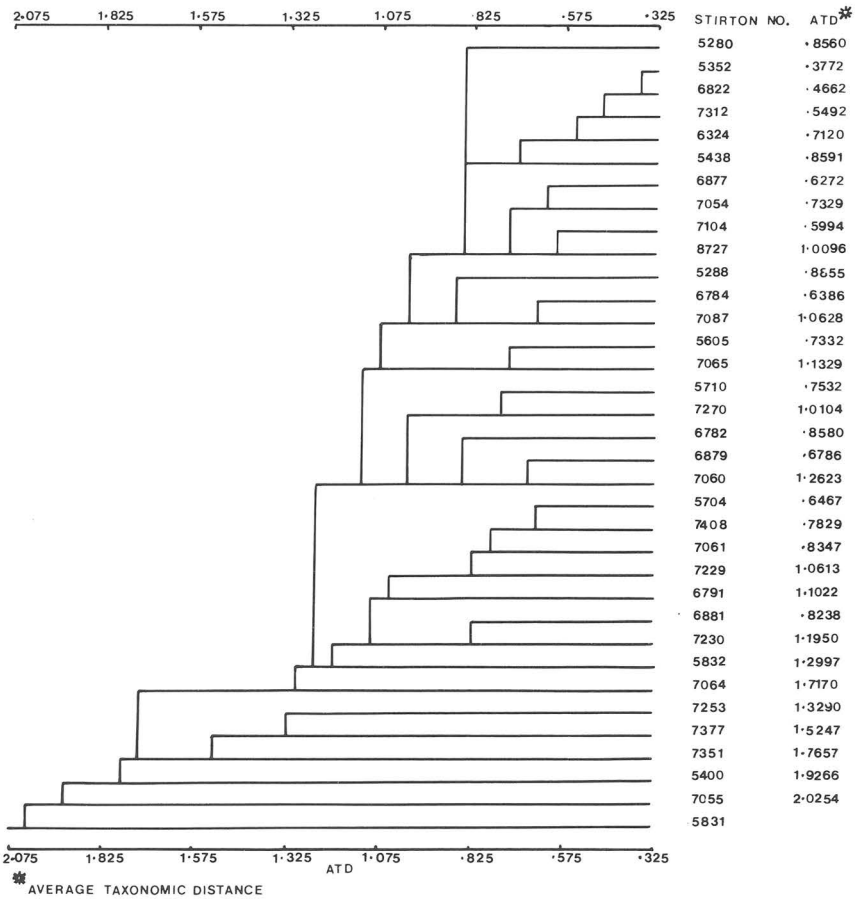

Figure 9 Cytological based dendrogram of 2n = 44 chromosome *Lantana camara* plants.

Table 5 Chromosome associations per cell in 2n = 33 chromosome plants

Chromosome association	5759	6837	6875	6878	6883	7067	7348	7381	7382	7383	7384	7387	7393	7394	7398	Total
$16_{II}1_{I}$						1										1
$15_{II}3_{I}$						1										1
$15_{II}1_{III}$						1		8		4						13
$14_{II}5_{I}$						2										2
$14_{II}2_{I}1_{III}$								3		1			3			7
$13_{II}4_{I}1_{III}$								3	1	4	2					10
$13_{II}1_{I}2_{III}$					2	3	3	5	2	6		3	1	1		26
$12_{II}6_{I}1_{III}$													1	1		2
$12_{II}3_{I}2_{III}$		2	2			1			5			4	3	3	4	24
$12_{II}3_{III}$													1	1		2
$11_{II}8_{I}1_{III}$											1					1
$11_{II}5_{I}2_{III}$				3					5		4		2	1	3	18
$11_{II}2_{I}3_{III}$		2	2		4	6	2	1		1	1	5	2	1		27
$10_{II}13_{I}$													4	2		6
$10_{II}7_{I}2_{III}$			1						2		1	1				5
$10_{II}4_{I}3_{III}$	1	1		6	3	4				1	3	1	3	2	8	33
$10_{II}1_{I}4_{III}$		1	1	1	2											5
$9_{II}6_{I}3_{III}$							3		2		2				2	9
$9_{II}3_{I}4_{III}$	4	4	2	9	8	1	7				1	6			3	45
$9_{II}5_{II}$		1														1
$8_{II}8_{I}3_{III}$			1								4			1		6
$8_{II}5_{I}4_{III}$			1													1
$8_{II}2_{I}5_{III}$	3	3	3	1	1				1							12
$7_{II}10_{I}3_{III}$									1							1
$7_{II}7_{I}4_{III}$		1											2			3
$7_{II}6_{I}3_{III}1_{IV}$	1										1					2
$7_{II}4_{I}5_{III}$	1															1
$7_{II}1_{I}6_{III}$	4	2							1							7
$7_{II}5_{III}1_{IV}$							1			1						2
$6_{II}6_{I}5_{III}$		1	1							1			2	3		8
$6_{II}3_{I}6_{III}$	4		2										1	2		9
$6_{II}7_{III}$							2									2
$5_{II}11_{I}4_{III}$			1													1
$5_{II}8_{I}5_{III}$										1				2		3
$5_{II}5_{I}6_{III}$	2		2				1							1		6
$5_{II}2_{I}7_{III}$	1						1							4		6
$4_{II}4_{I}7_{III}$	1	2	5													8
$4_{II}2_{I}5_{III}2_{IV}$			1													1
$3_{II}3_{I}8_{III}$	3															3

Table 6 The minimum spanning tree for 2n = 33 chromosome plants

Stirton no.	Stirton no.	ATD
5759	6837	1,504
6837	6883	0,986
6883	6878	0,564
6878	7398	0,652
6883	7387	0,711
7398	7382	1,006
7387	7348	1,081
7387	7383	1,082
7383	7381	0,832
7387	7067	1,13
7398	7384	1,91
7398	7393	1,237
7393	7394	1,115
6837	6875	1,475

3. The 2n = 44 chromosome group

The 35 plants in this group showed a wide variety of cytological features. Univalent percentages varied from 1,64% in *Stirton 7351* to 9,77% in *Stirton 7087* with an average of 5,27% (Table 7). The bivalent frequency varies from 39,45% in *Stirton 5831* to 82,26% in *Stirton 7351* with an average of 59,96%. From an average of 14,18% trivalents values varied between 2,18% in *Stirton 7055* and 23,38% in *Stirton 7230*. The quadrivalent frequency varied from 6,36% in *Stirton 7253* to 33,82% in *Stirton 7055*. Pentavalents and hexavalents were frequently encountered in several plants.

The data used for numerical taxonomic purposes resulted in four cytogroups being identified within the *L. camara* specimens with 44 somatic chromosomes.

3.1 Group θ

This group is composed of *Stirton 5280, 5352, 5438, 6324, 6882, 6877, 7054, 7104, 7312* and *8727*. *Stirton 5280, 5352, 5438* and *8727* were collected in Natal, *Stirton 6822, 6877, 7054, 7104* and *7312* were collected from the White River complex and *Stirton 6324* was collected near Mossel Bay.

Group θ has an average chromosome association of $2{,}4_{I}\ 12{,}9_{II}\ 1{,}7_{III}\ 2{,}6_{IV}\ 0{,}01_{V}\ 0{,}004_{VI}$ and a chiasma frequency of 1,16 (s = 0,05) (Table 7). Most cells approach a $12_{II}\ 5_{IV}$ type chromosome association but associations vary from 22_{II} to $6_{II}\ 8_{IV}$ (Table 8).

3.2 Group ι

This group consists of *Stirton 5288, 5710, 6782, 6784, 6879, 7060, 7087, 7270* and *7377*. *Stirton 5288* was collected in Natal, *Stirton 5710* was collected near Tzaneen and the rest of the plants were all collected from the White River hybrid swarm.

Group ι has an average chromosome association of $2{,}8_{I}\ 14{,}7_{II}\ 1{,}9_{III}\ 1{,}5_{IV}\ 0{,}009_{V}$ and an average chiasma frequency of 1,1 (s = 0,04) (Table 7). There is a marked increase in bivalent formation and a decrease in quadrivalent formation when compared with group θ. The decrease in chiasma frequency is also significant. The chromosome associations per cell vary from 22_{II} to $6_{II}\ 8_{IV}$ with $14_{II}\ 4_{IV}$ as the most frequent form (Table 8).

3.3 Group κ

The components of this group are *Stirton 5605, 5704, 6791, 7061, 7064, 7065, 7229, 7230* and *7408*. *Stirton 5605* was collected in Natal and *Stirton 5704* near Nylstroom, whereas the rest of these plants came from the White River complex. With an average chiasma frequency of 1,23 (s = 0,06), this group has an average chromosome association of $2_{I}\ 11{,}7_{II}\ 2{,}6_{III}\ 2{,}6_{IV}\ 0{,}03_{V}\ 0{,}008_{VI}$ (Table 7). The increase in multivalents over both θ and ι is reflected in the significant increase in chiasma frequency. The chromosome associations vary from 22_{II} to $4_{II}\ 9_{IV}$ with the majority of the cells having $14_{II}\ 4_{IV}$ to $8_{II}\ 7_{IV}$ (Table 8).

3.4 Group λ

This group consists of all the plants not included in any other group of the 2n = 44 chromosome group. These plants include *Stirton 5400, 5831, 5832, 6881, 7055, 7253* and *7351*. *Stirton 5400* was collected in Natal, both *Stirton 5831* and *5832* were collected in the Western Cape, *Stirton 7253* was

Table 7 Chromosome associations and chiasma frequencies in 2n = 44 chromosome plants

Stirton no.	2n=	No. cells analysed	% of Chromosomes bound as I	II	III	IV	V	VI	Number of chiasmata/ bivalent
5280	44	25	5,36	60	12,82	21,82	—	—	1,14
5288	44	25	9	66,73	11,18	13,09	—	—	1,1
5352	44	25	4,59	64	14,68	16,73	—	—	1,13
5400	44	20	4,66	67,45	3,89	18,59	5,41	—	1,16
5438	44	25	4,82	66,73	7,09	20,36	0,45	0,55	1,16
5605	44	25	6,36	57,45	18,27	17,45	0,45	—	1,25.
5704	44	25	4,64	47,5	19,38	28,03	—	0,45	1,24
5710	44	25	5,36	62,73	17,18	13,82	0,91	—	1,13
5831	44	25	4,36	39,45	32,18	24	—	—	1,21
5832	44	25	6,27	52,18	17,18	24,36	—	—	1,15
6324	44	25	3,36	62,73	11,73	22,18	—	—	1,23
6782	44	25	7,06	69,41	12,26	11,27	—	—	1,14
6784	44	20	8,07	58,18	13,3	20,45	—	—	1,09
6791	44	25	4,73	41,82	21	32	0,45	—	1,23
6822	44	20	4,55	59,09	13,64	22,73	—	—	1,13
6877	44	20	7,13	57,49	9,17	26,21	—	—	1,12
6879	44	25	4,64	67,09	11,18	17,09	—	—	1,1
6881	44	25	6,91	59,82	22,36	10,91	—	—	1,11
7054	44	25	7,73	51,45	14,18	26,18	0,45	—	1,12
7055	44	25	4,09	56,36	2,18	33,82	1,36	2,18	1,23
7060	44	20	3,98	74,09	13,3	8,64	—	—	1,06
7061	44	25	3,91	53,82	17,45	24,36	0,45	—	1,23
7064	44	25	5,45	59,78	13,15	21,08	—	0,55	1,15
7065	44	25	6,18	53,45	19,91	20	0,45	—	1,16
7087	44	20	9,77	58,64	17,05	14,55	—	—	1,03
7104	44	25	5,55	54,73	11,73	28	—	—	1,24
7229	44	25	2,91	52,55	14,73	29,82	—	—	1,37
7230	44	25	2,81	55,12	23,38	17,04	1,64	—	1,24
7253	44	20	5,34	72,27	16,02	6,36	—	—	1,04
7270	44	20	4,43	67,05	18,07	10,45	—	—	1,1
7312	44	25	4,45	63,09	11,73	20,73	—	—	1,2
7351	44	25	1,64	82,26	3,28	12,37	—	0,45	1,14
7377	44	20	5,11	78,64	5,8	10,45	—	—	1,14
7408	44	20	3,07	56,59	13,98	26,36	—	—	1,23
8727	44	25	6,18	48,55	11,73	33,07	0,45	—	1,24
$\bar{x}$	44	23,57	5,27	59,96	14,18	20,12	0,34	0,13	1,16

collected near Pretoria and the representatives of the White River complex in this group are *Stirton 6881, 7055* and *7351*. These plants show no relationship with one another or with any plant in any other group with 44 somatic chromosomes.

4. The 2n = 55 and 66 chromosome groups

As only three 2n = 55 chromosome plants (*Stirton 5287, 7430* and *7432*) and two 2n = 66 chromosome plants (*Stirton 7058* and *7431*) were collected in this study, no attempt has been made to subdivide these plants.

5. Comparison of morphological and cytogenetical characters

It is unpractical to depend on cytological data alone for the classification of plants. Therefore, an attempt was made to find a correlation between the cytogenetic groupings and the morphological data. Since the α cytogroup consists of the most plants it was decided to use this group in an attempt to find a common morphological feature. Complete botanical descriptions of some plants classified in the α group (*Stirton 7066, 7069, 7308, 7338, 7374, 7389* and *7390*) were prepared by Stirton (1982). When these descriptions are compared with one another, the following morphological differences between the plants become evident.

The inflorescence is usually depressed ovate when young and very broadly ovate when older except in *Stirton 7374* where young inflorescences are flattened and older ones are depressed ovate. The width of the inflorescences varies from 20–25 mm in *Stirton 7338* to 25–30 mm in *Stirton 7066*. The length varies from 6–7 mm in *Stirton 7338* to 10 mm in *Stirton 7066* and *7308* when opening and from 9–10 mm in *Stirton 7389* to 20–25 mm in *Stirton 7069* when older. The flowering peduncle varies from 12–20 mm in *Stirton 7308* to 30–42 mm in *Stirton 7069*, whereas the fruiting peduncle varies from 30–35 mm in *Stirton 7308* to 45–60 mm in *Stirton 7389*.

The bracts may vary from 3,5–4 mm long in *Stirton 7308* to 6–8 mm in *Stirton 7069*. The width of the bract at the

widest point varies from 1 mm in *Stirton 7338* to 3 mm in *Stirton 7389*. The form of the bract varies from narrowly acutely spathulate through linear lanceolate and broadly lanceolate to triangular and triangular oblong.

Flower colour is usually orange (56%), but yellow (24%), pink (12%) and white and red (4% each) are also encountered. A variety of different shades of the same colour can be seen in different plants (Figure 13). As an example some different shades of yellow will be discussed. The flowers may open and close a pale yellow colour with a golden eye (B1:5:2:1 with eye E3:7:1,5 according to the colour chart of Biesalski) in *Stirton 7338* (Figure 13e). The flowers of *Stirton 7374* (Figure 13g) have a uniform yellow colour (F2:6,5:1 — Biesalski) from opening to closing. A more intense yellow (F3:7:1 — Biesalski) was found in both opening and closing flowers of *Stirton 7389* (Figure 13h). The shade differences, in particular the orange and pink forms where the opening and closing and sometimes even the intermediate flowers have different colours, are much more complex than those differences described in the yellow-flowered plants.

Although the lateral margin of the flower is always convex, the apex varies from strongly convex to straight. The base angle varies from 15° in *Stirton 7380* to 40° in *Stirton 7374*. The calyx varies from 2 mm long in *Stirton 7069, 7308* and *7390* to 3 mm in *Stirton 7389*. The calyx is bilobed in each plant with the lobes somewhat toothed in *Stirton 7308* and *7060*.

From the above-mentioned morphological differences it is obvious that group α is not a morphologically homogeneous group. These morphological differences are emphasized by the fact that Stirton (pers. comm.) has classified the plants in group α into 12 different cultivars. Likewise group β is divided into four cultivars and group γ into three cultivars. As if the whole situation is not complicated enough, the morphological resemblance is not restricted to one cytogroup. In this way *Stirton 7293* (α), *7302* (γ), *7306* (β) and *7369* (γ) represent a single morphological cultivar (Stirton 1984).

Table 8 Adapted chromosome associations per cell in 2n = 44 chromosome plants (the correct number of univalents are added to trivalents to form quadrivalents. The additional univalents are added to the bivalent frequency. This was done in an attempt to delimit the number of associations and to see the tendency of multivalent formation in the plant)

Plant no. (*Stirton*)	22_{II}	$20_{II}1_{IV}$	$18_{II}2_{IV}$	$16_{II}3_{IV}$	$14_{II}4_{IV}$	$12_{II}5_{IV}$	$10_{II}6_{IV}$	$8_{II}7_{IV}$	$6_{II}8_{IV}$	$4_{II}9_{IV}$
5280	2	2	–	3	1	12	3	2	–	–
5288	–	2	4	12	4	3	–	–	–	–
5352	–	–	4	6	5	7	2	1	–	–
5400	1	4	4	5	2	4	–	–	–	–
5438	1	1	3	9	5	6	–	–	–	–
5605	–	2	–	7	2	8	1	–	5	–
5704	–	–	–	–	4	6	7	5	1	2
5710	–	1	3	2	12	4	–	2	1	–
5831	–	–	–	–	–	–	5	8	9	3
5832	–	–	–	1	8	3	11	2	–	–
6324	–	–	4	3	7	7	4	–	–	–
6782	1	5	6	3	3	5	1	1	–	–
6784	–	–	–	5	6	9	–	–	–	–
6791	–	–	–	–	1	4	3	13	3	1
6822	–	–	2	4	4	5	2	3	–	–
6877	–	2	1	4	3	6	1	3	–	–
6879	–	1	6	5	8	2	3	–	–	–
6881	1	1	1	4	6	5	2	4	1	–
7054	–	–	1	3	7	5	4	3	2	–
7055	–	–	–	12	4	4	2	1	1	1
7060	–	3	3	7	7	–	–	–	–	–
7061	1	–	3	1	6	1	3	6	2	2
7064	3	2	1	2	5	5	3	1	–	3
7065	–	1	–	6	4	2	5	2	5	–
7087	–	1	1	5	5	5	2	1	–	–
7104	–	–	–	5	6	7	3	4	–	–
7229	–	–	–	4	6	3	4	4	3	1
7230	–	–	–	1	6	7	3	8	–	–
7253	5	6	–	2	6	1	–	–	–	–
7270	–	–	–	5	14	1	–	–	–	–
7312	–	–	3	6	5	10	1	–	–	–
7351	1	13	–	10	1	–	–	–	–	–
7377	3	3	7	5	2	–	–	–	–	–
7408	–	–	2	1	4	6	5	1	–	1
8727	–	–	–	1	5	10	1	8	–	–
Total	19	50	59	149	174	163	81	83	33	14

Table 9 The minimum spanning tree for 2n = 44 chromosome plants

Stirton no.	Stirton no.	ATD
5280	6877	0,457
6877	6784	0,615
6784	7087	0,714
7087	5288	0,648
5288	7060	0,585
7060	6879	0,709
7060	7270	0,628
7270	5710	0,776
6879	5352	0,607
5352	7312	0,711
7312	6324	0,632
6324	7408	0,688
7408	5704	0,756
5704	6791	0,701
6791	5831	0,73
5831	7061	0,707
6791	8727	0,658
8727	7104	0,802
5831	7065	0,64
5704	7229	0,619
6879	7377	0,603
7377	6782	0,757
5352	6822	0,579
6791	7230	0,575
5704	5832	0,573
5832	7054	0,596
7060	7351	0,571
7065	5605	0,568
7377	7253	0,546
7312	5438	0,526
5438	7055	0,615
7230	6881	0,516
7351	5400	0,392
7061	7064	0,387

These differences are not restricted to the 2n = 22 chromosome plants. The four plants in group δ represent four different morphological cultivars, the two plants in both groups ϵ and ζ two morphological cultivars each and all three morphologically studied plants in group η represent three morphological cultivars. To further complicate things *Stirton 7348* of group η is placed in the same morphological cultivar as *Stirton 5352* of group θ. Thus plants on different ploidy levels are morphologically similar. This relationship cannot be tested cytologically but is theoretically possible.

The four plants studied morphologically in both groups θ and ι represent in both cases different morphological cultivars. Six plants of the group κ were morphologically studied and they represent four different morphological

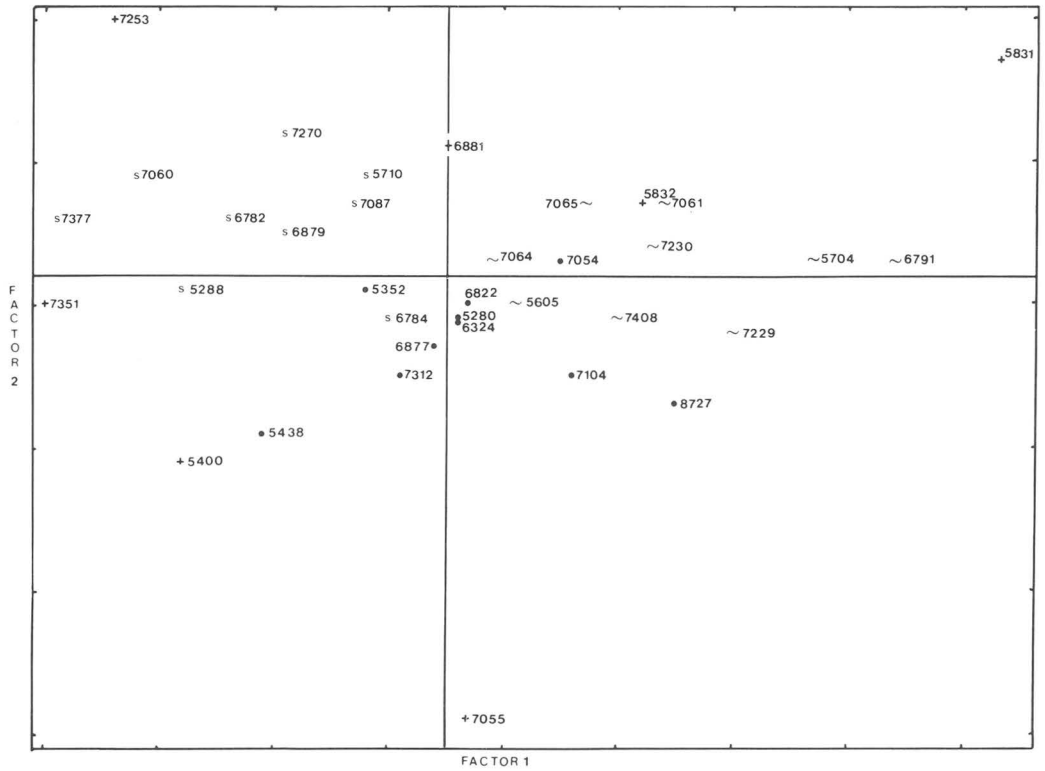

Figure 10 Cytological based principal component analysis of 2n = 44 chromosome *Lantana camara* plants.

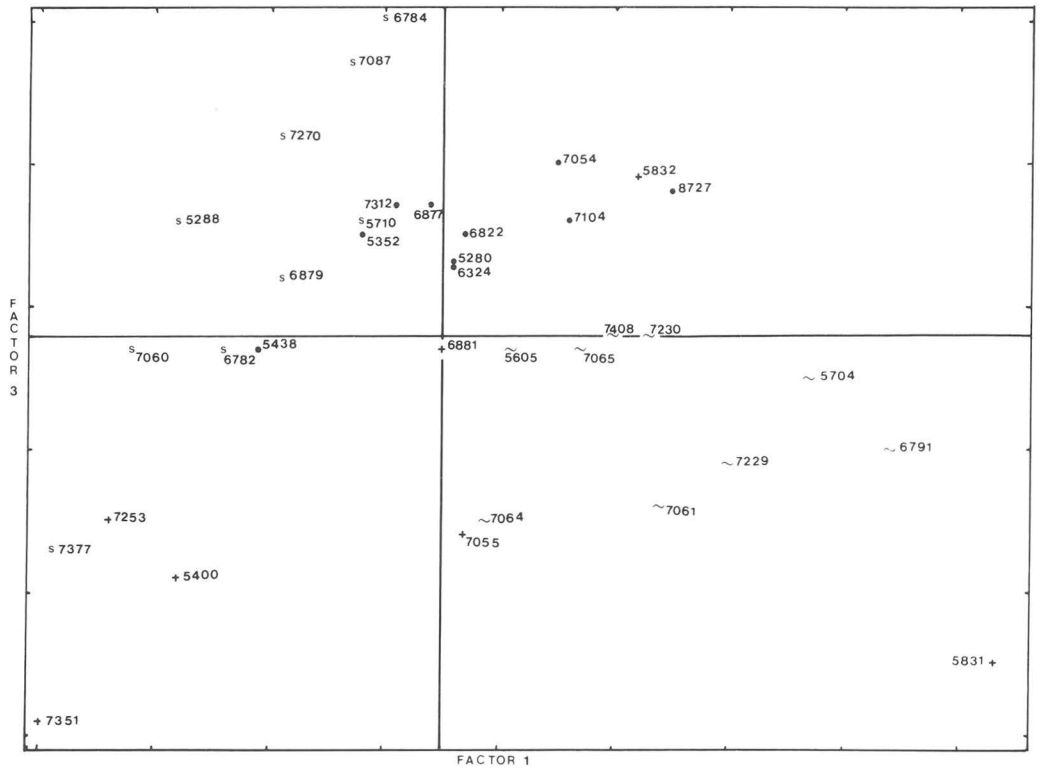

Figure 11 Cytological based principal component analysis of 2n = 44 chromosome *Lantana camara* plants.

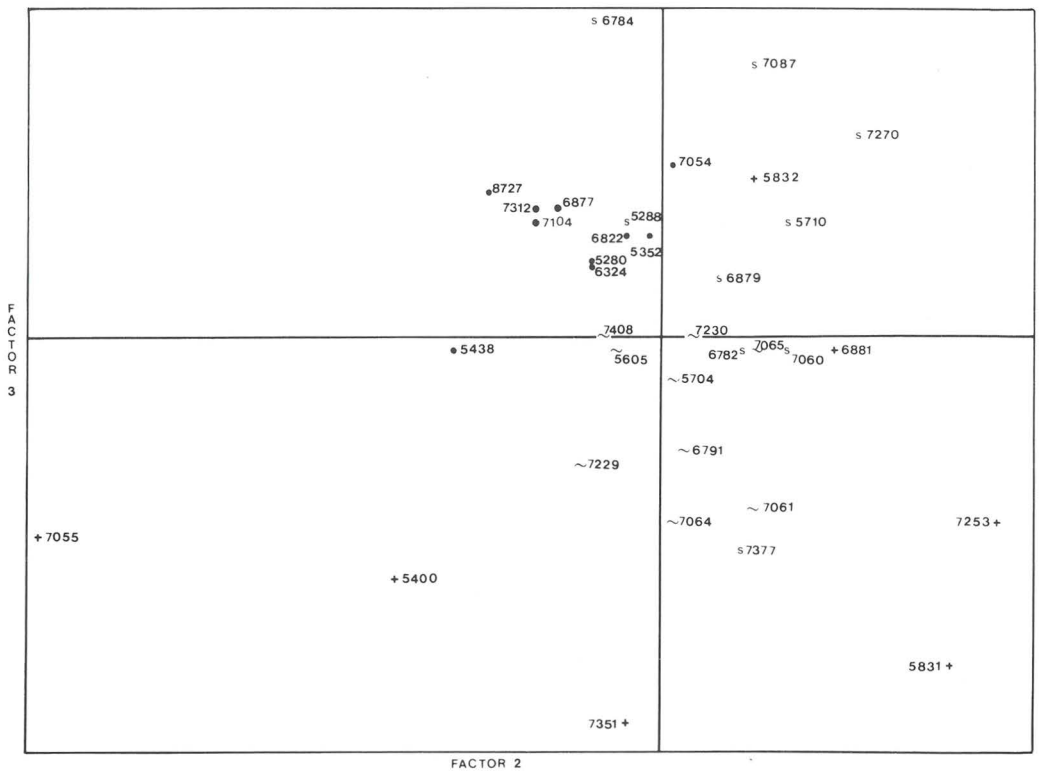

Figure 12 Cytological based principal component analysis of 2n = 44 chromosome *Lantana camara* plants.

cultivars. Intergroup relationships were present in *Stirton 5605* (κ) and *5832* (λ), as well as in *Stirton 6791* (κ) and *7377* (λ). Group λ can be divided into four morphological cultivars according to the five studied plants (Stirton 1984).

The differences observed between cytological and gross morphological data are also present ultrastructurally as seen with the scanning electron microscope. *Stirton 7066, 7303* and *7374* of the α group were studied (Figure 14). All three plants have prickle hairs on their abaxial petal surfaces. In addition to these prickle hairs *Stirton 7303* and *7374* have glandular trichomes and a wrinkled epidermis. The adaxial petal surfaces of *Stirton 7066* and *7303* are covered with papillae, the ones in *Stirton 7066* are pungent whereas those in *Stirton 7303* are acuminate. The adaxial petal surface in *Stirton 7374* is, in addition to having acuminate papillae, raised into a series of 'wart-like' outgrowths in contrast to the flat epidermal surface of *Stirton 7066* and *7303*. The abaxial leaf surfaces of *Stirton 7303* and *7374* are covered with prickle hairs and glandular trichomes, whereas *Stirton 7066* has long macro-hairs in addition to these other structures. *Stirton 7066* and *7374* have long macro-hairs and sessile glandular trichomes on the stem and *Stirton 7303* has, in addition, stalked glandular trichomes and long macro-hairs.

An ultrastructural investigation of *Stirton 5605, 6791* and *7408* of the κ group of the 2n = 44 cytodeme revealed the same type of intergroup variation (Figure 15). The abaxial petal surface of both *Stirton 5605* and *7408* are covered with prickle hairs and glandular trichomes, whereas *Stirton 6791* has no such structures. The adaxial petal surface of *Stirton 5605* consists of low-domed papillae but regular papillae are visible in both *Stirton 6791* and *7408*. *Stirton 5605* and *6791* have long macro-hairs on the abaxial leaf surfaces. In contrast *Stirton 7408* has only prickle hairs and glandular trichomes. The stem of *Stirton 5605* is covered with long macro-hairs, whereas the stems of *Stirton 6791* and *7408* are devoid of macro-hairs.

6. *Lantana camara* in South Africa

The occurrence of *Lantana camara* in South Africa can be traced back to 1858 in Cape Town and 1883 in Durban (Stirton 1977; Wells & Stirton 1981). The exact taxa that were introduced are not known and it is still not known whether the widespread forms encountered today are typical descendants of the parental forms or whether they are hybrids better adapted to local conditions.

If the slim chances of production of new morphological forms by mutations are ignored, either a totally heterozygous plant or at least two differing parental forms of *L. camara* must have been introduced. This deduction is based on the assumption that flower colour is regulated by at least two alleles where, in its simplest form AA represents red, Aa pink and aa white, whereas BB adds yellow to the potential genetic colour spectrum. AABB and AaBb will, therefore, result in orange flowers whereas aaBB will produce yellow flowers. This is an over-simplification of the inheritance of flower colour in *L. camara* but it does illustrate the lowest number of genes possible and gives an indication of the complexities involved.

The existing flower colour spectrum was, therefore, formed as a result of segregation of the genes responsible for flower colour in self-pollinated heterozygous offspring and by recombination in different forms after hybridization. The same principle applies to all other morphological criteria (eg. thorniness, form of flower and leaves, growth habit, etc.). From the above it appears highly unlikely that only one or two highly heterozygous or totally different plants were originally introduced. It is, therefore, suggested that many different forms were introduced at different times and hybridization has resulted in the present morphological

variation.

This variation in morphological characters is an indication of the extent of hybridization in *L. camara*. In a randomly pollinated population, the genes for different characters will, in the absence of linkage, be sorted in all possible combinations. In such a case the formula 2^n, where n represents the number of characters, will give the number of different phenotypes possible if each of the chosen characters is controlled by a single pair of alleles with total dominance. As a result, the larger the number of characters used, the greater the number of 'taxonomically distinguishable entities' there will be. The total number of possibilities (2^n) will not be found in nature because linkage will occur to some extent and the number of combinations will always be slightly less

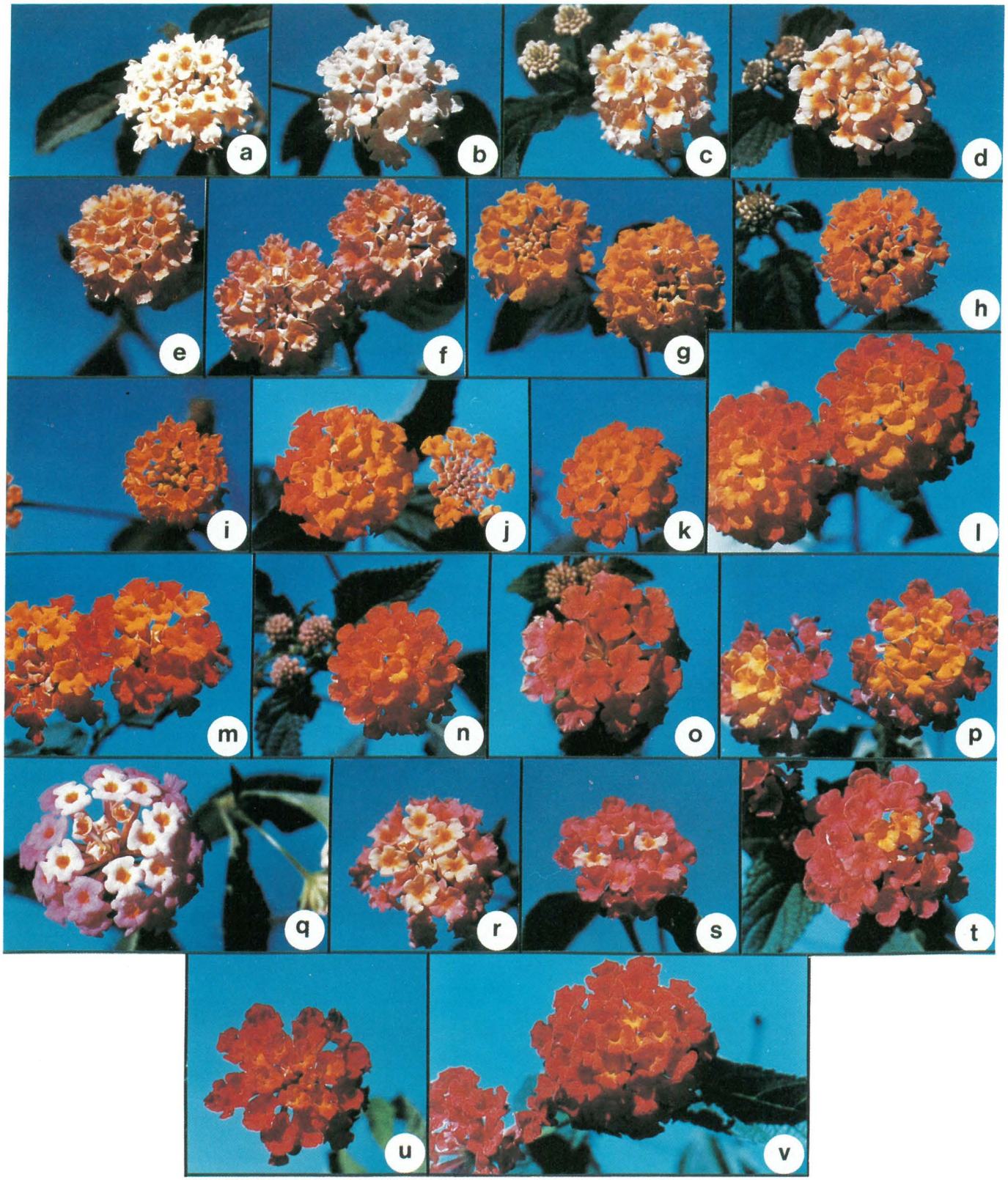

Figure 13 Flower colour variation in *Lantana camara*. *Stirton* collection numbers and cytogroup classification of reference material. a. *7062* (α); b. *7398* (δ); c. *7316* (α); d. *7343* (α); e. *7338* (α); f. *7294* (α); g. *7374* (α); h. *7389* (α); i. *7068* (γ); j. *6878* (δ); k. *7390* (α); l. *7303* (α); m. *7066* (α); n. *7308* (α); o. *7394* (ζ); p. *7071* (α); q. *7067* (η); r. *7069* (α); s. *7399* (α); t. *7393* (ζ); u. *6883* (δ); v. *7305* (α).

than 2^n. However, the number will still be too high to regard each recombinant as a separate taxonomic entity. This renders traditional taxonomy, where such groups are subdivided into infraspecific or specific entities, useless in randomly pollinating populations with a wide spectrum of morphological differences.

The infraspecific classification of *L. camara* is, as mentioned above, problematic. The most acceptable infraspecific classification is the delimitation of *L. camara* into five varieties (Moldenke 1973). The principal criterion for the recognition of the varieties *nivea* (Vent.) L.H. Bailey, *mista* (L.) L.H. Bailey, *mutabilis* (Hook.) L.H. Bailey and *flava* (Medic.) Moldenke, as well as *L. camara* L. *sensu stricto*, is flower colour.

The hypothetical example described demonstrates the futility of using flower colour in a natural classification of *L. camara* and is largely the reason why taxonomists like Linnaeus (1753), Sprengel (1825), Bailey (1949), Moldenke (1973) and several others have had no real success at infraspecific classification. All the taxonomic keys in the above classifications were based on either flower colour (Linnaeus 1753; Moldenke 1973) or thorniness (Sprengel 1825).

Since traditional taxonomic methods are virtually useless in classifying hybrid swarms, attention has been focussed on

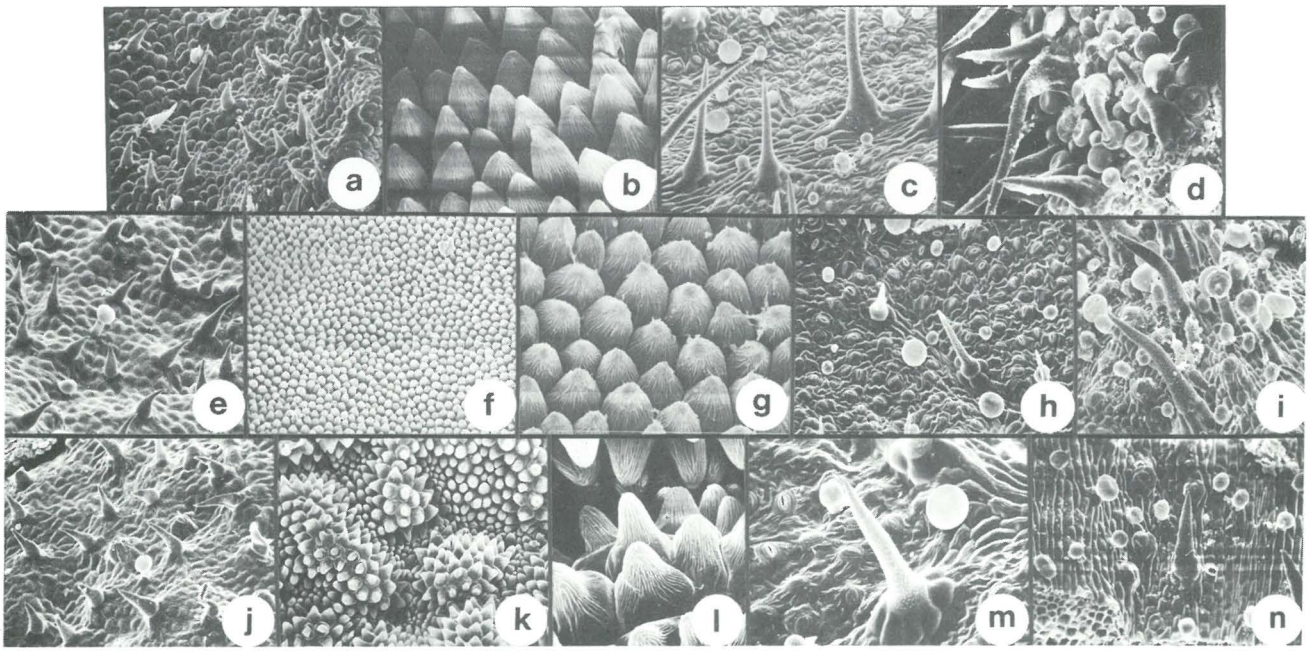

Figure 14 Ultrastructure of *Stirton 7066* (a–d), *7303* (e–i) and *7374* (j–n) of the α group. a, e & j. Abaxial petal surfaces (×240); b, f, g, k & l. Adaxial petal surfaces (f & k ×240; b, g & l ×1200); c, h & m. Abaxial leaf surfaces (c & h ×240; m ×420); d, i & n. Stem surfaces (×240).

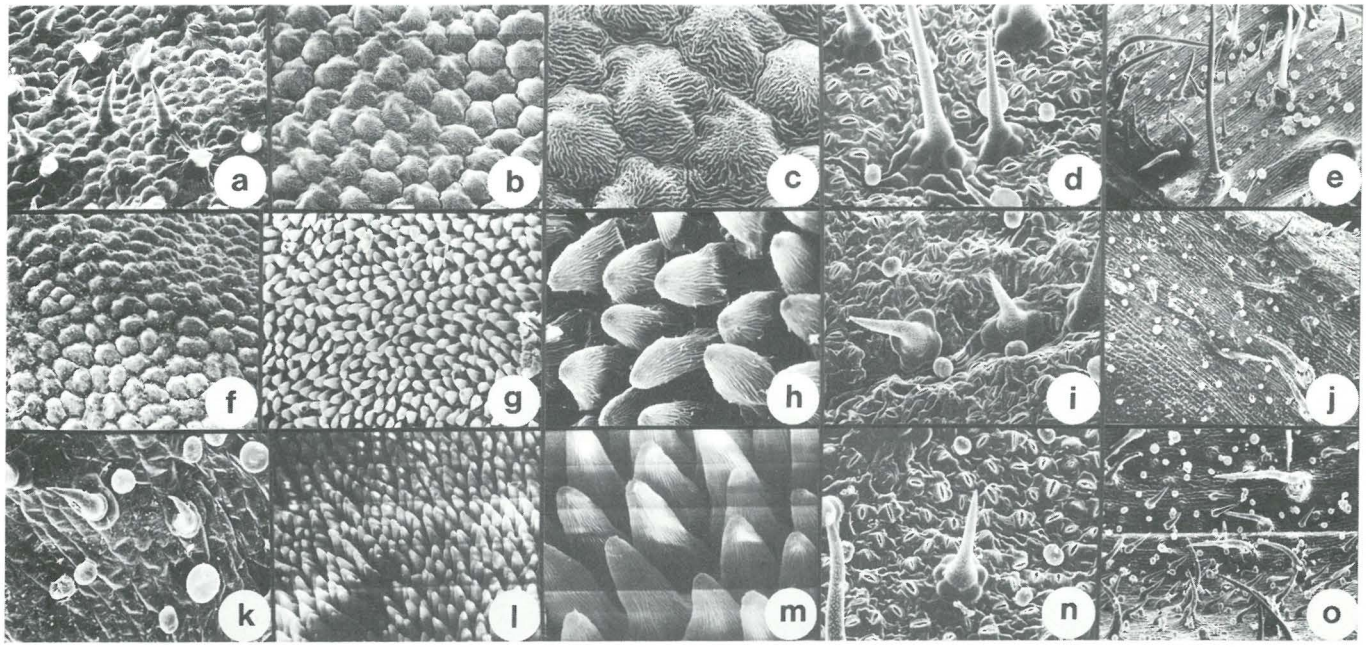

Figure 15 Ultrastructure of *Stirton 5605* (a–e), *6791* (f–j) and *7408* (k–o) of the κ group. a, f & k. Abaxial petal surfaces (×240); b, c, g, h, l & m. Adaxial petal surfaces (g & l ×240; b ×420; c, h & m ×1200); d, i & n. Abaxial leaf surfaces (×240); e, j & o. Stem surfaces (×60).

cytology as a possible means for the classification of hybrid offspring. Cytological data can be viewed in two separate ways for the purpose of taxonomy. The data can be used as additional morphological data (for example the chromosome number carries the same weight as the number of anthers and chromosome morphology makes the same contribution as flower or leaf morphology), or the chromosome behaviour during meiosis can be used to indicate the relationship between different plants (Stace 1980). For cytotaxonomical purposes, chromosomal characteristics will, therefore, be more important than morphological criteria.

6.1 Chromosome number and chromosome morphology

The most basic cytological data obtained during a cytological investigation concern the chromosome number. Chromosome numbers indicate that *L. camara* is a polyploid species with a basic chromosome number of x = 11 (Tandon & Chandi 1955) with diploid, triploid, tetraploid, pentaploid and hexaploid derivatives (Schnack & Covas 1947; Tjio 1948; Singh 1951; Sen & Sahni 1955a & b; Tandon & Bali 1955; Tandon & Chandi 1955; Natarajan & Ahuja 1957; Choudhary & Roy 1982; Spies & Stirton 1982b & c; Spies 1984e).

In addition to the basic chromosome number of x = 11 found in *L. camara* and several other *Lantana* species (Tjio 1948; Lewis 1961; Malik & Ahmad 1963), certain *Lantana* species have a basic chromosome number of x = 12 (Patermann 1935; Natarajan & Ahuja 1957; Arora 1960; Henderson 1969). The genus *Lantana* is, therefore, dibasic. This phenomenon is, however, not unique in the Verbenaceae as the genus *Verbena* is also dibasic with x = 5 and 7 (Darlington & Wylie 1955; Fedorov 1969).

Lantana is not the only genus in the Verbenaceae with a basic chromosome number of 11. Both *Nyctanthes* and *Avicennia* contain species with multiples of 11 (Raghavan & Arora 1960; Sharma & Mukhopadhyay 1963). The chromosome number alone is, therefore, of little importance as a taxonomical criterion for *Lantana camara*. However, the polyploid status of this species further complicates the use of the chromosome number in the taxonomy of the *L. camara* complex and suggests an additional biosystematical problem.

Species can be defined as groups of actually or potentially interbreeding natural populations, which are reproductively isolated from other such groups (Mayr 1942). If this is so, then strictly speaking different polyploid levels can be regarded as being different species since different polyploid levels are at least partially isolated with regard to reproduction.

Mayr (1957) described morphologically identical populations with either a sympatric or allopatric distribution as being sibling species as long as they are reproductively isolated. It would, therefore, seem that each polyploid level found in a population, must be regarded as another sibling species in the strictest sense of this definition. However, the application in practice is unpractical and this is one case where traditional taxonomic treatment must still be used and morphologically identical populations must be considered as the same taxon regardless of reproductive isolation and other considerations.

The fertility of uneven polyploid levels in *L. camara* (Spies 1984e) and the frequent hybridization between different ploidy levels (Spies 1984d) indicate that reproductive isolation between different polyploid levels in this species is not complete (Spies 1984d & e). The different polyploid levels of *L. camara* can be regarded as different cytodemes at most, especially as the polyploid level in most angiosperms is not correlated with any morphological character (Löve 1951; Lawrence 1970; Stace & Auquier 1978; Stace 1978 & 1980).

Chromosome morphology is usually a criterion highly valued by most taxonomists. In *L. camara* metacentric to submetacentric chromosomes with a length variation of 1,5–2,5 μ are found (Tjio 1948; Sharma & Mukhopadhyay 1963; Spies 1984e). The variation between chromosomes is not great enough to construct a meaningful karyotype or idiogram and consequently no taxonomically significant information can be obtained in this way.

6.2 Chromosome behaviour during meiosis

Homologous chromosomes pair during the meiotic process, whereas nonhomologous chromosomes cannot pair. A study of chromosome pairing helps to determine the degree of homology between different genomes. In this way autoploids (multiplication of homologous genomes) can be distinguished from alloploids (multiplication of non-homologous genomes after interspecific hybridization) or even segmental alloploids (multiplication of homoeologous genomes after hybridization of partially related plants) (Jackson & Casey 1980 & 1982; Jackson & Hauber 1982; Spies 1984a & e).

The determination of genome homology through the study of meiotic chromosome behaviour reflects the true relationships between plants. A prerequisite for the above-mentioned is the absence of any influence by gene action on chromosome pairing (Riley 1966). Multivalents are formed in *L. camara* and, therefore, no such genes are present in this species. By determination of genome homology the cytogroups α to λ were identified and defined. The significance of these groups will now be discussed.

(a) The 2n = 22 chromosome groups. The implication of the occurrence of trivalents and quadrivalents on the ploidy status of these supposedly diploid plants has previously been investigated (Spies & Stirton 1982c; Spies 1984a & e; 1985). It was found that *L. camara* had a basic chromosome number of x = 5 + (5 + 1), with two homologous genomes, consisting of five chromosomes each (Spies 1984e; 1985).

In group α trivalents were observed in only 6,45% of the examined cells whereas 88,1% of the cells had at least 10 bivalents. From this observation it can be concluded that the diploidization process in the 2n = 22 plants (see Spies 1984e), is most advanced in this group. Therefore, the α group can be considered in an evolutionary sense as the most advanced group at the 2n = 22 chromosome level.

As the diploidization process is not as advanced in the β group as it is in the α group, the β group is, in an evolutionary sense, much more primitive than the α group. However, the diploidization process has commenced in the β group because these plants do not correspond with autoploid plants any longer. This deduction is based on the fact that fewer multivalents than can be expected theoretically, were observed.

Since the plants in the β group are in a transitional stage from autoploidy to secondary diploidy through diploidiza-

tion, they do not share a distinct set of cytogenetic characters. Distinction between plants in the β group and γ group (the nonclustered plants) is only possible by using all the characters available. Although these plants are grouped together in the analysis, the clustering is only the product of statistical manipulation, as plants with more or less similar average values were grouped together. The only recognizable group in the 2n = 22 chromosome plants is, therefore, the α group.

The 2n = 22 chromosome plants can be separated into plants where diploidization has reached its climax (group α) and plants in different stages of diploidization (groups β and γ). As this process is continuing, the transitional plants are intermediate in all respects and no cytotype (or morphotype) can yet be identified. Recognition of infraspecific taxa is, therefore, not possible.

(b) The 2n = 33 chromosome plants. Quadrivalents, or a total of more than 11 bivalents and multivalents per cell, were encountered in 83,44% of the cells studied in this group. This is further proof that the 2n = 33 plants are not autotriploid plants but higher polyploids because true autoploids could have produced a maximum total of 11 bivalents and trivalents and no quadrivalents.

The same phenomenon was described by Choudhary & Roy (1982) who found 15 bivalents in 2n = 33 *L. camara* plants in India. The only other way (other than a lower basic chromosome number than 11) in which a genome consisting of 11 chromosomes can form four bivalents, is when translocations occurred in eight chromosomes resulting in homoeology between four pairs. The probability that 72,73% of the chromosomes in a genome could undergo such specific translocations appears very unlikely. Therefore, this high occurrence of a greater number of bivalents and multivalents than is theoretically predicted must result from a lower basic chromosome number. This has been previously demonstrated (Spies 1984a & e; 1985) to x = 5 + (5 + 1).

The highest frequency of bivalents and lowest frequency of multivalents were encountered in the ϵ group.

The ζ group exhibits a variability of chromosome associations and a significant drop in chiasma frequency (1,06 compared to δ with 1,14 and ϵ with 1,12). The drop in

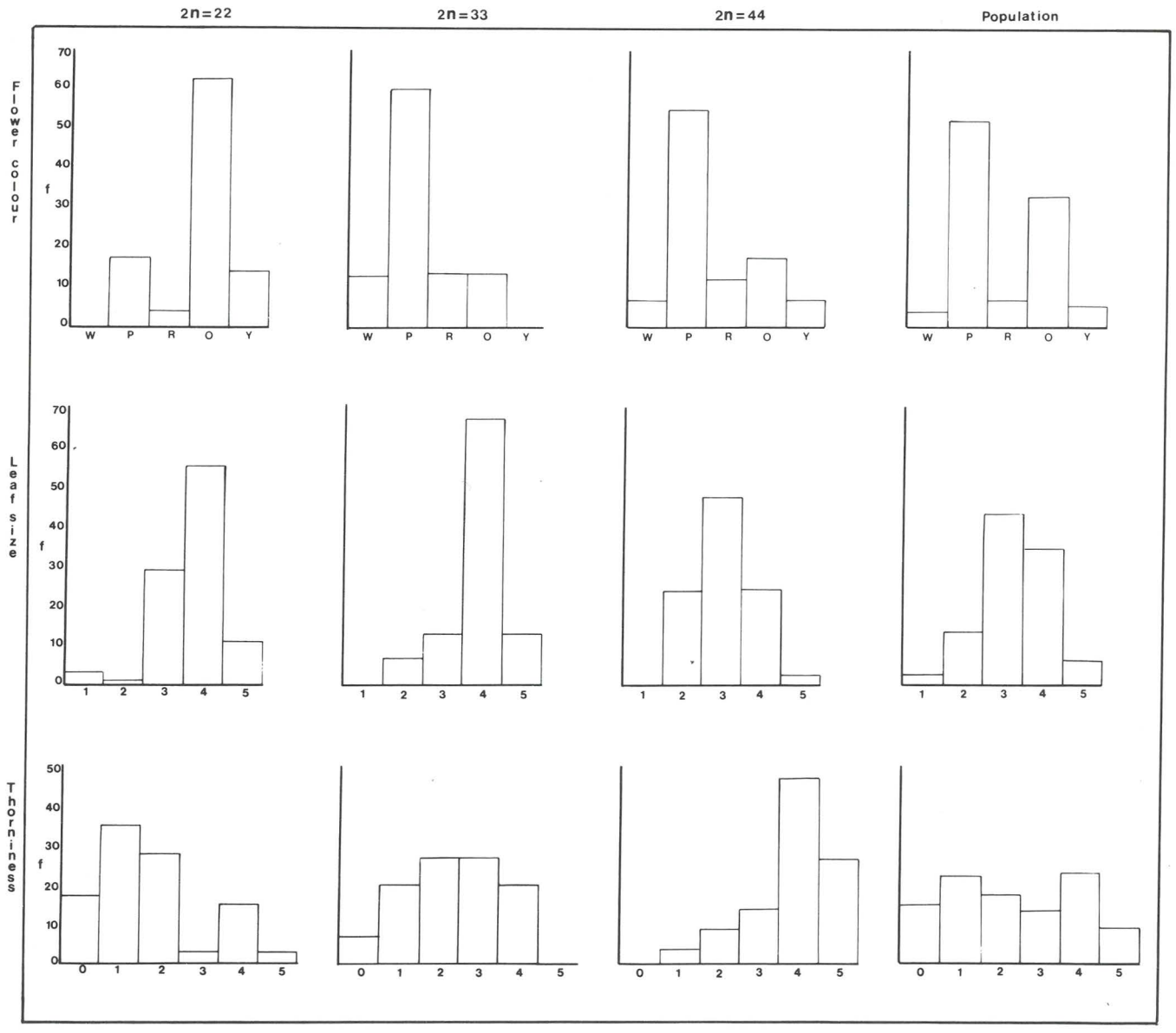

Figure 16 Comparison between polyploid level and flower colour, leaf size and thorniness in *Lantana camara*.

chiasma frequency indicates a lesser degree of genome homology.

(c) The 2n = 44 chromosome group. The formation of pentavalents and hexavalents, as well as the high frequency of multivalents formed, indicates that this group is not tetraploid but includes higher polyploid levels (Spies 1984a & e; 1985) and again confirms the lower basic chromosome number for *L. camara*.

The κ group had a lower bivalent frequency and higher multivalent frequency than any other 2n = 44 group. This fact, combined with the very high chiasma frequency, indicates a high degree of genome homology in these plants. Since multiplication of more genomes is involved in the 2n = 44 plants than in the 2n = 22 plants, it is much more difficult to deduce the evolutionary pathway of the higher polyploids. The combined effect of diploidization, multiplication of genomes and hybridization increases the complexity of the higher polyploids and makes attempts to determine phylogenetical relationships almost impossible.

Although group θ has fewer multivalents and more bivalents than the κ group, it also has more multivalents than an autotetraploid plant can theoretically have (Spies 1984a). Therefore, this group also represents a higher autoploid level. The ι group represents a case of segmental alloploidy with its higher frequency of bivalents and lower frequency of multivalents.

Furthermore, it is interesting to note that *Stirton 6791* (κ) and *7377* (λ) are both classified as *L. camara* var. *nivea*. Both South African plants have 44 somatic chromosomes, compared with the 22 (Natarajan & Ahuja 1957) described in their Indian equivalent. The Indian *nivea* plants formed

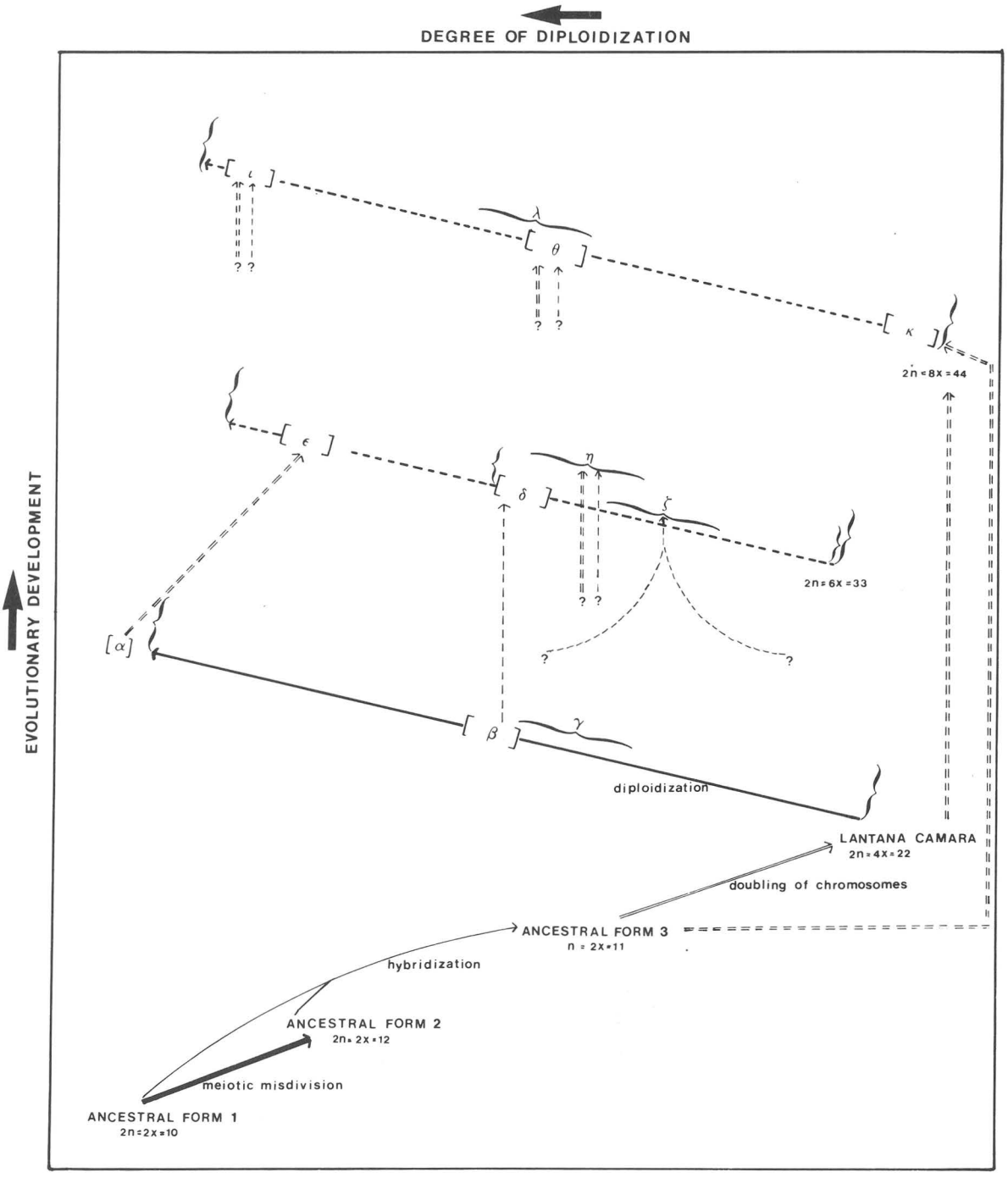

Figure 17 Proposed evolutionary development in the *Lantana camara* complex based on cytological data.

only bivalents (Natarajan & Ahuja 1957) and this corresponded with the α group, whereas its South African counterparts varied in their meiotic behaviour. This fact is further proof that no taxonomical treatment is yet possible.

As a result of the above-mentioned differences between the cytological data and morphological data, an attempt was made to find a correlation between polyploid level and certain morphological characters (Figure 16). From Figure 16a it can be seen that 2n = 22 chromosome plants are the only group where more orange than pink flowers were observed. Although this tendency is present, the occurrence of other than orange flower colours at 2n = 22 level and the occurrence of orange flower colour at higher ploidy levels, renders flower colour to be of little practical taxonomical use.

Furthermore, no correlation between leaf size and ploidy level could be found (Figure 16b). The tendency for thorniness to increase with an increase in ploidy level (Figure 16c) is of little use for the same reasons as described for flower colour. Even the combined effect of flower colour and thorniness is suppressed by the sporadic occurrence of thorny pink 2n = 22 and of thornless orange 2n = 44 chromosome plants.

Conclusions

Several different genetic forms of *Lantana camara* have been introduced into South Africa. Through the processes of hybridization, polyploidization and diploidization, an incredibly variable complex has been formed. At this stage, taxonomy based on morphology has not succeeded in classifying infraspecific taxa. This is not surprising as the cytological data indicate that this complex is still undergoing an active evolutionary phase and that the majority of plants are in a transitional stage from the ancestral form to an evolved secondary diploid form (Figure 17). Only the plants in cytogroup α are approaching stability and will, therefore, form the basis for a new species or infraspecific entity.

The cytological data were successful in the delimitation of phytogenetical relationships, thus indicating that *L. camara* has an aneuploid autoploid origin. The cytogenetic data further delimited the α group which can be used as a basis for taxonomic treatment. The cytogenetic data demonstrated that the South African *L. camara* population is in the process of active evolution and continuous monitoring of this group might add to our knowledge of the evolutionary process.

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